



ORIGINAL
ARTICLE



Dispersal and ecological traits explain differences in beta diversity patterns of European beetles

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ABSTRACT

Aim Disentangling the contributions of niche and dispersal processes as species distribution drivers is crucial from both theoretical and practical standpoints. We investigated whether niche-related and dispersal-related functional traits of 19 beetle clades were good predictors of beta diversity patterns across continental European countries.

Location Continental Europe.

Methods We quantified the overall compositional heterogeneity (a measure of multiple-site dissimilarity) of each beetle clade in continental Europe and assessed its relationship with body size and the proportion of wingless species as proxies for dispersal ability. Overall compositional heterogeneity was also compared with trophic and habitat preferences of clades as proxies for their ecological specialization. Additionally, beta diversity patterns were characterized as a multivariate pairwise dissimilarity matrix among pairs of countries for each beetle clade. We assessed whether differences among these pairwise structures were related to dispersal ability or the ecological specialization of clades. The turnover and nestedness-resultant components of compositional dissimilarity were calculated separately for all analyses.

Results The dispersal ability and ecological specialization explained a large proportion (> 70%) of the variation in overall compositional heterogeneity but a lower proportion (c. 40%) of the variation in the multivariate pairwise structures. Remarkably, the explained variation was shared between both sets of predictors in the case of overall compositional heterogeneity but was independently related to dispersal ability or ecological specialization for the multivariate pairwise structure analysis.

Main conclusions These results suggest a tight relationship between ecological specialization, dispersal ability and compositional heterogeneity of European beetle clades. However, the specific patterns of dissimilarities between pairs of countries seem to be determined independently by either ecological or dispersal processes and seem to be subject to other unmeasured factors.

Keywords

Beta diversity, Coleoptera, cross-taxon congruence, dispersal, ecological traits, Europe, nestedness, turnover.

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INTRODUCTION

Understanding the factors that control species distributions and, hence, biodiversity patterns is a principal objective in

ecology and biogeography. Established theoretical alternatives invoke completely different processes to explain species distributions and biodiversity patterns. Niche theory assumes a mechanistic control of species distributions by the environ-

ment (Hutchinson, 1957), whereas neutral theory emphasizes the role of stochastic dispersal, speciation and extinction processes (Hubbell, 2001). However, the relative importance of alternative paradigms is difficult to assess because most macroecological patterns are consistent with multiple theories. Classic examples are the distance decay of similarity, which can be explained by either niche differentiation or spatial isolation (Nekola & White, 1999; Tuomisto *et al.*, 2003), and the latitudinal richness gradient, which could be generated by species niche conservatism and niche differentiation (Hawkins *et al.*, 2003, 2006; Wiens, 2007) or by limited post-glacial recolonization (Svenning & Skov, 2007; Baselga *et al.*, 2012).

A potential way to move forward in assessing the relative importance of dispersal and niche processes in controlling species distributions is to compare the biogeographical patterns of clades with different functional characteristics (Soininen *et al.*, 2007b; Qian, 2009; Jiménez-Valverde *et al.*, 2010). If we can identify functional traits linked either to dispersal ability or to niche requirements, we can assess whether the variation in functional traits among clades is related to the variation in biogeographical patterns. In other words, we ask the question: do clades with different dispersal abilities or different niches present different biodiversity patterns? If so, is variation in biodiversity patterns among clades better explained by dispersal- or niche-related traits (assumed to account for dispersal and niche processes, respectively)? This approach differs from typical analyses which consider the drivers of biodiversity patterns where the cases are spatial units, the dependent variable is species richness (or species composition) of spatial units, and the predictors are the spatial unit characteristics (e.g. latitude/longitude or environmental conditions). For the approach proposed in the present study, the cases are clades, the dependent variable is the biogeographical pattern of clades across the full study area, and the predictors are the functional traits of the clades.

In this study, we focus on beta diversity patterns of beetle clades and assess whether these patterns are correlated with variations in dispersal or niche-selection associated traits. The term 'beta diversity' can be defined in different ways (Tuomisto, 2010; Anderson *et al.*, 2011); we refer to both the compositional dissimilarity among multiple sites for a given clade (hereafter referred to as 'overall compositional heterogeneity') and the multivariate structure resulting from pairwise compositional dissimilarities between specific sites (i.e. a spatial dissimilarity matrix for a clade; hereafter referred to as 'multivariate pairwise structure'). Therefore, the beta diversity differences among clades can be represented in two different forms. First, the overall compositional heterogeneity (i.e. the degree of dissimilarity of all the spatial units taken together) can be compared between clades. For example, if dispersal was the key process controlling species distributions, overall compositional heterogeneity should be higher in less vagile clades (Qian, 2009;

Baselga *et al.*, 2012). Second, the multivariate pairwise structure of compositional dissimilarities could also be compared between clades (Fig. 1). For example, clades with identical overall compositional heterogeneity (e.g. beetles and arachnids in Fig. 1) may present a different multivariate pairwise structure (i.e. the composition of assemblages in sites 1 and 2 is very similar in the beetles but completely dissimilar in the arachnids). These differences may result from different speciation, extinction or colonization processes linked to niche or dispersal processes. Therefore, it is possible to investigate whether clades with different functional traits show (1) different overall compositional heterogeneity, and/or (2) different multivariate structures in their pairwise dissimilarity matrices. Relatively few studies have explored the relationship between overall compositional heterogeneity and functional traits associated with dispersal (e.g. Steinitz *et al.*, 2006; Qian, 2009) or niche processes (e.g. Soininen *et al.*, 2007a). Those studies that did explore this relationship usually lacked statistical power owing to the limited number of biological groups compared (but see Soininen *et al.*, 2007a,b). Moreover, we are not aware of any attempts to explore the covariation between functional traits and the multivariate structure of assemblage variation patterns (i.e. do clades with similar traits have similar pairwise dissimilarity matrices?). We therefore propose a novel method for assessing the variation in clades' multivariate pairwise structures and its correlates. This method is based on a clade-focused matrix summarizing the differences in the multivariate pairwise structures of beetle clades (i.e. clade versus clade distance matrix). This novel clade distance matrix is used as a dependent variable against the functional traits of clades.

Beetles are an excellent subject for this analysis because we can obtain distributional and functional information for many diverse clades with different traits (potentially linked to dispersal abilities and ecological strategies) while maintaining reasonable homogeneity of physiological constraints, body sizes and morphologies. This relative homogeneity helps to characterize the functional traits of different clades within a common framework, thus avoiding the comparison between completely disparate organisms. For example, the energetic dispersal costs are known to decrease with body size in insects (Roff, 1977), but this relationship is not necessarily maintained across organisms with different locomotion modes (e.g. passive versus active dispersal, see Martiny *et al.*, 2006) or with varying body sizes (Soininen *et al.*, 2007a). The empirical information of actual dispersal rates in beetles is extremely scarce, but available evidence from capture-recapture experiments at the landscape scale shows that individuals of larger species disperse between habitat patches more frequently than those of smaller species (Roslin, 2000). Similarly, the ability to fly may not relate to dispersal ability when comparing such divergent groups as microbes and vertebrates. However, within beetles, flightlessness has been shown to impact dispersal ability even at evolutionary scales,

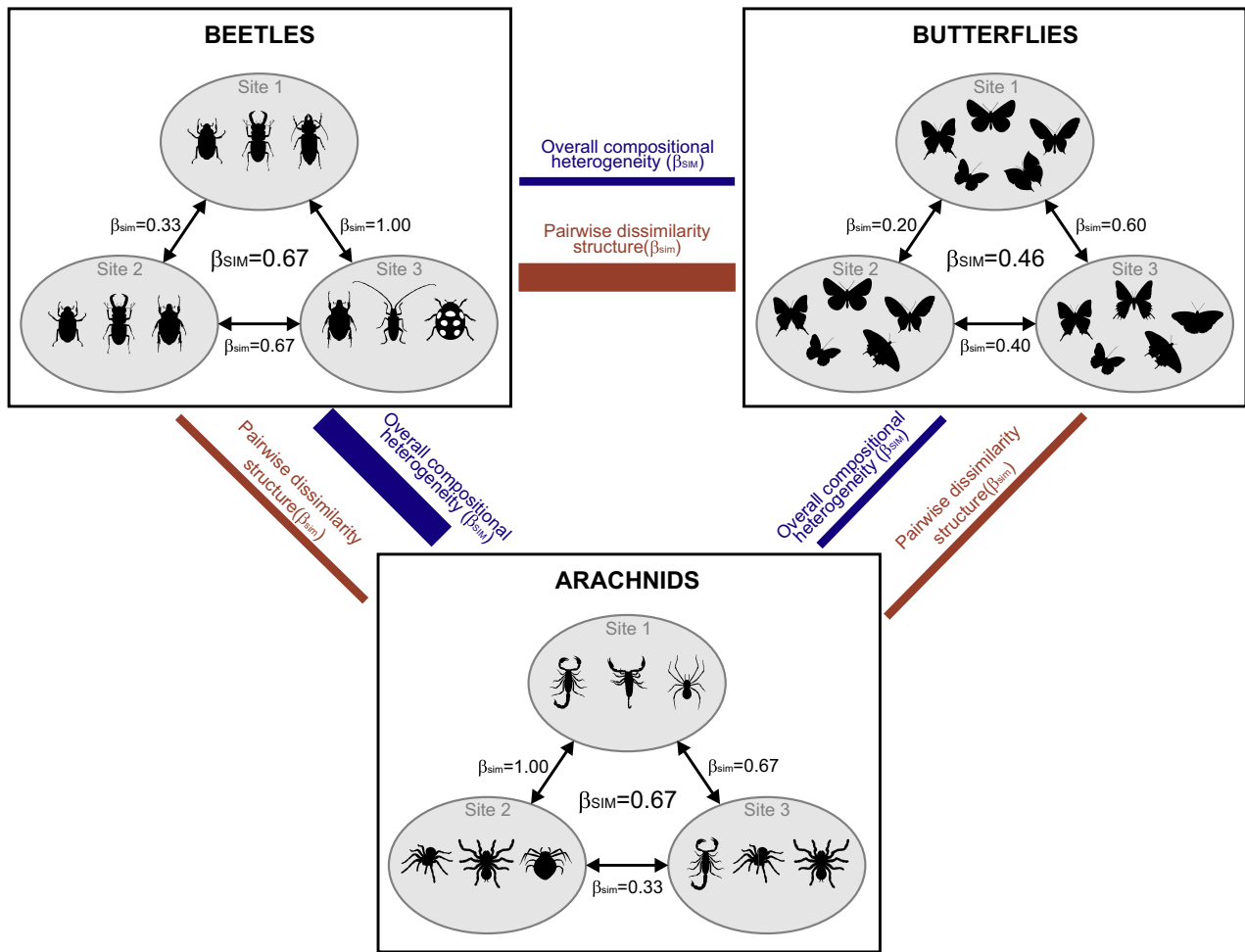


Figure 1 Hypothetical beta diversity patterns for three different clades (beetles, butterflies and arachnids) across three different sites (sites 1–3). Beetles and arachnids show identical values of overall compositional heterogeneity ($\beta_{SIM} = 0.67$ for both) but poorly correlated multivariate pairwise dissimilarity patterns ($r^2 = 0.25$). For example, the composition of sites 1 and 2 is completely dissimilar in arachnids but very similar in beetles. In contrast, beetles and butterflies have very different overall faunistic heterogeneity values ($\beta_{SIM} = 0.67$ for beetles, $\beta_{SIM} = 0.46$ for butterflies) but perfectly correlated multivariate pairwise dissimilarity patterns ($r^2 = 1.00$). Numerical values correspond to the specific, idealized patterns shown in the figure, but these patterns are arbitrary (i.e. not based on empirical observations or theoretical expectations).

increasing allopatric speciation (Ikeda *et al.*, 2012) and reducing (or even preventing) the colonization of previously glaciated areas (Drees *et al.*, 2010; Schuldt & Assmann, 2011). Regarding traits related to ecological niche processes, habitat and trophic specialization have obvious implications for species distributions according to niche theory (Hutchinson, 1957); however, their effects could not be comparable across organisms with very different physiological constraints. Within beetles, habitat selection and trophic position relate to variations in abundance, richness and composition of local beetle assemblages (e.g. Davies *et al.*, 2000; Binckley & Resetarits, 2005; Driscoll & Weir, 2005). At larger scales, these local processes must influence species distributions via multiple paths (e.g. the large-scale distribution of habitats or the reduction of extinction probability in more generalist taxa). In sum, the relative morphological and

physiological homogeneity across different beetle clades should minimize mismatches between the functional traits and the involved processes.

In the present study we aim to evaluate the relationship between beta diversity (overall heterogeneity and multivariate pairwise structure) and functional traits using distributional and functional data for 19 European beetle clades (see Table 1). We have characterized beta diversity patterns for each beetle clade by separating the turnover and nestedness-resultant components of dissimilarity. Thus, we have differentiated the pattern resulting from the substitution of species between sites (spatial turnover) from that resulting from the loss of species from site to site in a subset pattern (nestedness) (Baselga, 2010, 2012, 2013). For each clade, the patterns of both beta diversity components were characterized as (1) the overall compositional

Table 1 The beetle clades from continental Europe included in this study. The family, number of species, main habitat, trophic specialization, proportion of apterous species and mean size, following Baselga *et al.* (2012), are included. For semiquantitative variables, the rank order used in the analyses is provided in parentheses. The ordering was based on the spread of habitats (the epiedaphic habitat being the most widespread and the epiphytic habitat the most patchy) and the specificity of trophic requirements (coprophagous/necrophagous being the least and herbivorous the most specific).

Clade	Species number	Apterous species (%)	Mean size (mm)	Main habitat	Trophic specialization	Family
<i>Amara</i>	135	13	7	Epiedaphic (1)	Phytophagous (4)	Carabidae
Apionidae	287	0	3	Epiphytic (4)	Phytophagous (4)	Apionidae
<i>Carabus</i>	120	98	25	Epiedaphic (1)	Zoophagous (2)	Carabidae
Cerambycinae	134	0	15	Epiphytic (4)	Xylophagous (3)	Cerambycidae
<i>Chaetocnema</i>	33	6	2	Epiphytic (4)	Phytophagous (4)	Chrysomelidae
Hydraenini	158	0	2	Aquatic (3)	Phytophagous (4)	Hydraenidae
Lamiinae	300	53	14	Epiphytic (4)	Xylophagous (3)	Cerambycidae
Lepturinae	119	0	11	Epiphytic (4)	Xylophagous (3)	Cerambycidae
Limnebiini	43	0	2	Aquatic (3)	Phytophagous (4)	Hydraenidae
Ochtebiini	135	0	2	Aquatic (3)	Phytophagous (4)	Hydraenidae
<i>Otiorhynchus</i>	698	100	9	Epiedaphic (1)	Phytophagous (4)	Curculionidae
Phyllobiini	93	0	5	Epiphytic (4)	Phytophagous (4)	Curculionidae
Polydrusini	134	0	4	Epiphytic (4)	Phytophagous (4)	Curculionidae
Pselaphinae	817	32	2	Edaphic (2)	Zoophagous (2)	Staphylinidae
<i>Pterostichus</i>	241	82	16	Epiedaphic (1)	Zoophagous (2)	Carabidae
Scarabaeidae	93	0	14	Epiedaphic (1)	Coprophagous (1)	Scarabaeidae
Scolytinae	236	0	3	Epiphytic (4)	Xylophagous (3)	Curculionidae
Silphidae	40	15	17	Epiedaphic (1)	Necrophagous (1)	Silphidae
<i>Trechus</i>	253	94	5	Edaphic (2)	Zoophagous (2)	Carabidae

heterogeneity across all European territories, and (2) the multivariate pattern of pairwise dissimilarities between European territories. Subsequently, we studied the differences in beta diversity patterns among clades and assessed whether differences were related to dispersal or ecological traits.

MATERIALS AND METHODS

Data

Species presence/absence of 19 beetle clades (large genera, tribes, subfamilies or families; 4064 species in total) in 34 European territories (11° W–60° E and 36° N–72° N) was compiled from Löbl & Smetana (2003) for *Amara*, *Carabus*, *Pterostichus* and *Trechus*; from Löbl & Smetana (2004) for Pselaphinae and Silphidae; from Danilevsky (2007) for Cerambycinae, Lamiinae and Lepturinae; from Löbl & Smetana (2010) for *Chaetocnema*; and from the Fauna Europaea Web Service (available online at <http://www.faunaeur.org>, accessed in 2010) for Apionidae, Hydraenini, Limnebiini, Ochthebiini, *Otiorhynchus*, Phyllobiini, Polydrusini, Scarabaeidae and Scolytinae. All of these sources report species presence in European countries and were coded as '1' in our final presence/absence table (see Appendix S1 in Supporting Information). The lack of documented presence in any given country was coded as an absence (0 in our table), but given the nature of these data sources, some of these absences may be proven false in the future. This dataset includes the most diverse

beetle superfamilies (Caraboidea, Staphylinoidea, Scarabaeoidea, Chrysomeloidea and Curculionoidea) and encompasses clades with different life strategies in terms of microhabitat, trophic specialization, and divergent dispersal abilities. In general, territories correspond to continental European countries (all islands are excluded from this study to avoid complex biogeographical patterns linked to insularity) although one country was split and two were pooled (Croatia and Bosnia-Herzegovina were pooled into a single unit because the former surrounds the latter, and European Russia was split into three units – north, central and south – given its extremely large area). The smaller (< 2000 km²) countries of Andorra, Liechtenstein, San Marino, Monaco and Vatican City were removed from the dataset to avoid extreme differences in area. Although data were also available for Luxembourg and Moldova, these countries were excluded from the analyses owing to the absence of some clades, which poses problems for computing faunal dissimilarity and comparing with the other territories. For this same reason, two clades included in a previous paper (Baselga *et al.*, 2012), namely Baridinae and Nanophyidae, were not considered in this study (absent in Albania, Slovenia and Macedonia).

Clades were classified according to their main habitat (i.e. epiedaphic, edaphic, aquatic and epiphytic) and trophic specialization (i.e. coprophagous, zoophagous, xylophagous, phytophagous) following Baselga *et al.* (2012). As proxies of dispersal ability, the proportion of apterous species and species mean size were also obtained from Baselga *et al.* (2012). Details are provided in Table 1.

Statistical analyses

In this study, we analysed the variation among clades in (1) overall compositional heterogeneity in Europe (a single value of multiple-site dissimilarity across all European territories), and (2) pairwise dissimilarities in faunal composition among territories (multivariate pairwise structure) in relation to the functional traits of beetle clades.

Beta diversity measures

Beta diversity can be governed by two different phenomena: spatial turnover (species replacement between sites) and nestedness of assemblages (ordered species loss between sites) (Baselga, 2010, 2012). Alternative methods for partitioning beta diversity are available (Legendre, 2014), but only Baselga's framework yields a replacement component truly independent of (i.e. not bounded by) species richness difference (Baselga, 2012; Leprieur & Oikonomou, 2014; Baselga & Leprieur, in press). Therefore, we analysed these components of dissimilarity separately using the partitioning framework proposed by Baselga (2010). In this framework, total dissimilarity (the Sørensen index, a monotonic transformation of beta diversity, i.e. gamma/alpha) is additively partitioned into two indices. The first one (the well-known Simpson dissimilarity) accounts for spatial turnover (i.e. dissimilarity associated with species replacement removing the effect of nested patterns). The second one is the nestedness-resultant dissimilarity which accounts for the dissimilarity associated with nested subsets (i.e. richness differences among assemblages given the condition of these being nested). For the overall compositional heterogeneity, we used the multiple-site dissimilarity indices, β_{SIM} and β_{SNE} , for the turnover and nestedness-resultant components, respectively,

$$\beta_{\text{SIM}} = \frac{\left[\sum_{i < j} \min(b_{ij}, b_{ji}) \right]}{\left[\sum_i S_i - S_T \right] + \left[\sum_{i < j} \min(b_{ij}, b_{ji}) \right]}$$

and

$$\beta_{\text{SNE}} = \frac{\left[\sum_{i < j} \max(b_{ij}, b_{ji}) \right] - \left[\sum_{i < j} \min(b_{ij}, b_{ji}) \right]}{2 \left[\sum_i S_i - S_T \right] + \left[\sum_{i < j} \min(b_{ij}, b_{ji}) \right] + \left[\sum_{i < j} \max(b_{ij}, b_{ji}) \right]} \times \frac{\sum_i S_i - S_T}{\left[\sum_i S_i - S_T \right] + \left[\sum_{i < j} \min(b_{ij}, b_{ji}) \right]}$$

where S_i is the total number of species in site i ; and S_T is the total number of species in all sites considered together; and b_{ij} , b_{ji} are the number of species exclusive from sites i and j , respectively, when compared by pairs.

For computing the pairwise dissimilarity matrices, we used the pairwise indices, β_{sim} and β_{sne} , for the turnover and nestedness-resultant components, respectively,

$$\beta_{\text{sim}} = \frac{\min(b, c)}{a + \min(b, c)}$$

and

$$\beta_{\text{sne}} = \frac{\max(b, c) - \min(b, c)}{2a + \min(b, c) + \max(b, c)} \times \frac{a}{a + \min(b, c)},$$

where a is the number of species common to both sites, b is the number of species that occur in the first site but not in the second, and c is the number of species that occur in the second site but not in the first.

Models for variation in multiple-site dissimilarity across clades

Linear regression models were used to assess which characteristics of the clades were related to their overall compositional heterogeneity. A single continent-wide dissimilarity value for each clade was the response variable and was computed as the multiple-site Simpson dissimilarity index (β_{SIM}) for the spatial turnover pattern and as the multiple-site nestedness-resultant dissimilarity (β_{SNE}) for the nestedness component using command *beta.multi* in R package *BETAPART* (Baselga & Orme, 2012). Two bivariate linear models were built to evaluate two different hypotheses: (1) that differences in beta diversity patterns are related to species dispersal ability (dispersal hypothesis); and (2) that differences in beta diversity patterns are related to species ecology (ecology hypothesis). To test the dispersal hypothesis, the proportion of apterous species and mean size were used as proxies for species dispersal ability and were included in the model as interacting explanatory variables. For the ecology hypothesis test, the main habitat and trophic specialization were used as surrogates for a clades' ecological specialization and were categorized from low to high specialization (see Table 1). This characterization is coarse due to data constraints, but even these broad categories should be clearly correlated with differences in beta diversity patterns if niche processes are a major determinant of species distributions. Finally, all significant variables in the bivariate models were included in a combined model in order to partition the variation explained by dispersal ability and by ecological attributes. All these statistical models were independently conducted for the spatial turnover and nestedness-resultant components.

Models for variation in multivariate pairwise structure across clades

The variation in the multivariate pairwise structure across clades was evaluated using a clade distance matrix built from the correlation values (i.e. Pearson's r) between spatial dissimilarity matrices of all clades (see Fig. 2). That is, a clade distance matrix was computed for each component of beta diversity [i.e. turnover (β_{sim}) and nestedness-resultant (β_{sne})] following four steps [described in full only for the turnover component (β_{sim})]. (1) For each clade, a pairwise dissimilarity matrix was built based on β_{sim} using the command *beta.pair* from *BETAPART* package (Baselga & Orme, 2012) for R (R Core Team, 2013). This resulted in 19 spatial dissimilarity

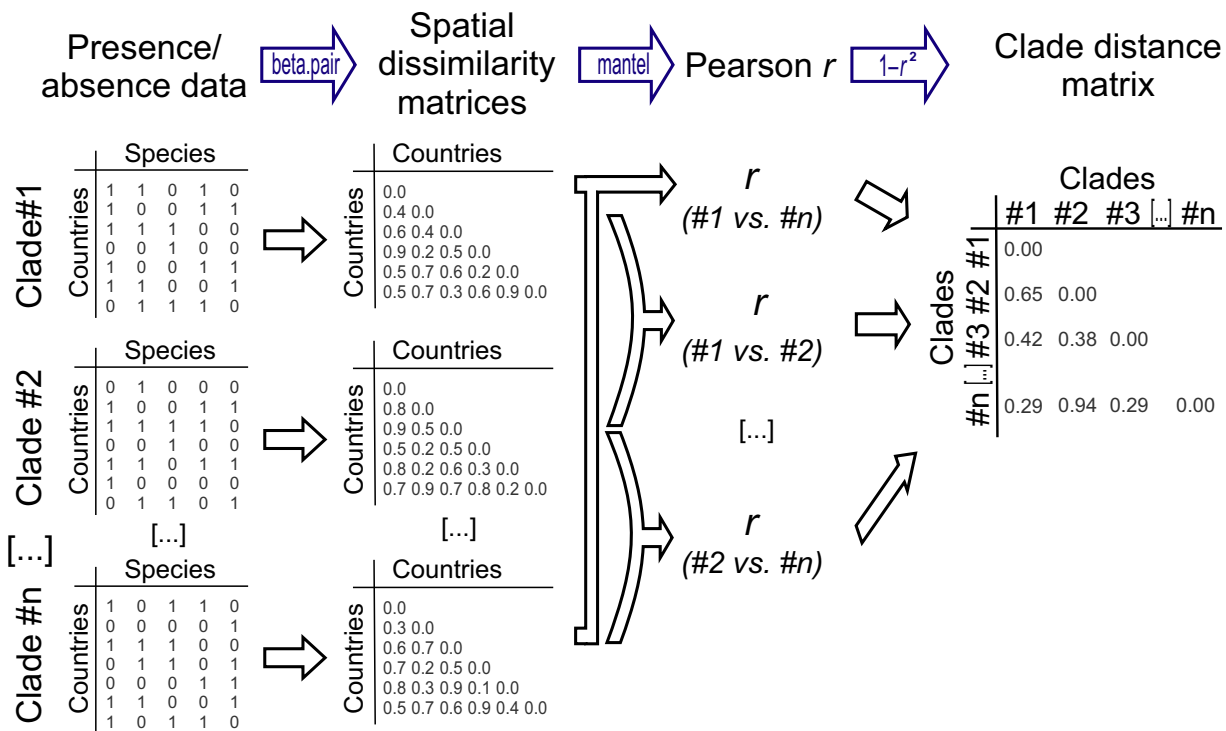


Figure 2 Scheme of the methodology applied to compute a clade distance matrix summarizing the variation in multivariate pairwise dissimilarity patterns across clades.

matrices, which was one for each clade. (2) For each pair of clades, the Pearson correlation between the spatial dissimilarity matrices was computed showing the congruence in the turnover pattern between those two clades. (3) Correlation values (Pearson's r) were transformed to distance values (Distance = $1 - r^2$) accounting for the degree of discrepancy in pairwise turnover patterns between two clades. (4) All distance values were compiled into a clade distance matrix summarizing the differences in the multivariate pairwise structure among clades for the turnover component of beta diversity. These same four steps were followed for the nestedness-resultant component (β_{sne}). To graphically represent the variation in multivariate pairwise structure among clades, a non-metric multidimensional scaling (NMDS) using command *metaMDS* in R package *VEGAN* (Oksanen *et al.*, 2013) was conducted on the resulting clade distance matrices, one for the turnover component and one for the nestedness component.

To evaluate the relationship between the variation in multivariate pairwise structure and the characteristics of the clades, a permutational multivariate analysis of variance (PERMANOVA) was conducted using command *adonis* in R package *VEGAN* (Oksanen *et al.*, 2013). This method allows the fitting of linear models to distance matrices to describe how variation in multivariate pairwise structures among clades is attributed to different covariates. As above, the proportion of apterous species and mean size, in addition to their interaction, were the potential predictors in the dispersal hypothesis. Main habitat and trophic specialization

were the potential predictors in the ecology hypothesis. The specific rank order of specialization had no effect on the amount of explained variation (not shown) because R computes linear, quadratic and cubic effects in linear models with ordered factors. All variables that were significant in the dispersal and ecology models were included in a combined model to partition the variation explained by dispersal or by ecological attributes. All these statistical models were conducted independently for the clade distance matrix based on the spatial turnover patterns and for the clade distance matrix based on the nestedness-resultant dissimilarity patterns.

Robustness of analyses to unequal country area

Finally, to assess the robustness of analyses to variations in territory areas, we replicated all analyses on a second dataset containing only territories greater than 100,000 km² ($n = 18$). In these supplementary analyses, overall compositional heterogeneity and multivariate dissimilarity patterns were computed for each clade among only these 18 larger territories, and the variation among clades was modelled using the clades' functional traits.

RESULTS

Differences among clades were evident in the values of overall compositional heterogeneity. The clades Scarabaeidae and Silphidae had the lowest replacement of species among

Table 2 Multiple-site dissimilarity values of species turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) components in beetles computed among all the territories studied in continental Europe.

	β_{SIM}	β_{SNE}
<i>Amara</i>	0.730	0.113
Apionidae	0.727	0.174
<i>Carabus</i>	0.822	0.087
Cerambycinae	0.701	0.172
<i>Chaetocnema</i>	0.694	0.161
Hydraenini	0.835	0.099
Lamiinae	0.747	0.142
Lepturinae	0.731	0.119
Limnebiini	0.825	0.091
Ochtebiini	0.851	0.087
<i>Otiorhynchus</i>	0.897	0.060
Phyllobiini	0.853	0.067
Polydrusini	0.817	0.103
Pselaphinae	0.849	0.089
<i>Pterostichus</i>	0.827	0.097
Scarabaeidae	0.637	0.246
Scolytinae	0.723	0.152
Silphidae	0.589	0.199
<i>Trechus</i>	0.906	0.057

territories (they had the lowest values of β_{SIM}) and the highest value of overall nestedness-resultant dissimilarity (Table 2). *Trechus* and *Otiorhynchus* showed the highest values of overall turnover and the lowest values of overall nestedness-resultant dissimilarity. A large proportion of variance in overall compositional heterogeneity was explained by dispersal and the ecological traits of beetle clades (75.6% for β_{SIM} and 72.4% for β_{SNE} ; Fig. 3a). Both the proportion of apterous species and body size were significant predictors within the dispersal hypothesis, while trophic specialization was the only significant variable within the ecology hypothesis for both components. The unique contribution of trophic specialization was larger than that of dispersal traits, particularly for the nestedness-resultant component. However, the larger fraction of explained variance was shared by both sets of predictors.

The assessment of the congruence in multivariate pairwise structures demonstrated that overall compositional heterogeneity and multivariate pairwise structures of clades do not necessarily vary in parallel. For example, Lamiinae and Scolytinae presented very similar values of overall compositional heterogeneity for both the turnover and nestedness components ($\beta_{SIM} = 0.747$ and 0.723 , respectively), but their multivariate pairwise structures were extremely different (Fig. 4, and see Appendix S2). In contrast, Scarabaeidae and Lamiinae had similar multivariate pairwise structures but different overall compositional heterogeneity. When we assessed the relationship between multivariate pairwise structures for each pair of clades, we observed a high variability in the strength of the relationship (r^2 between < 0.01 and 0.70). The NMDS showing the variation among clades in their multivariate

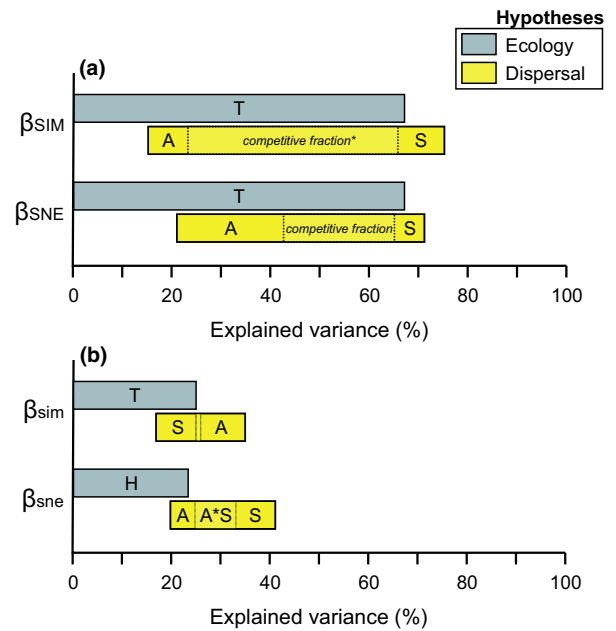


Figure 3 Percentage of variation in beta diversity patterns across beetle clades (in continental Europe) explained by functional traits in the ecology hypothesis [trophic trait (T) and habitat (H)] and dispersal hypothesis [size (S) and proportion of apterous species (A)]. (a) Linear regression analyses for the overall compositional heterogeneity [turnover (β_{SIM}) and nestedness-resultant dissimilarity (β_{SNE})]. (b) PERMANOVA analyses for the multivariate pairwise dissimilarity patterns [turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{sne})]. In analyses of overall compositional heterogeneity, the competitive fraction arises because the multiple regression ($\beta \sim A + S$) explains more variance than the sum of both individual models ($\beta \sim A$ and $\beta \sim S$), implying that both factors are competitive (see Legendre & Legendre, 1998, p. 534). In the multivariate pairwise analyses, the unique and shared contribution of each variable within the dispersal hypothesis is shown as well as the variance explained by the interaction of variables [A*S] when significant.

turnover patterns (Fig. 5a) revealed that although clades are not clustered, they are structured according to the measured traits. This result is evident in dimensions 1 and 2, which roughly reflect dispersal traits and trophic categories, respectively. With regard to nestedness-resultant dissimilarity patterns (Fig. 5b), no clear groupings were observed, but dimensions 1 and 2 were also roughly related to dispersal traits and habitat types, respectively. A formal analysis of these relationships (i.e. PERMANOVA analysis) revealed that both the ecological and dispersal attributes of clades had a relevant unique contribution to explain the differences among clades in their multivariate pairwise structure (Fig. 3b, total explained variance of 34.9% for β_{sim} and 40.9% for β_{sne}). In general, the proportion of variance explained by the ecology hypothesis was slightly larger than that explained by the dispersal hypothesis. The unique contributions of dispersal and ecological predictors were larger than the proportion of variance explained by both

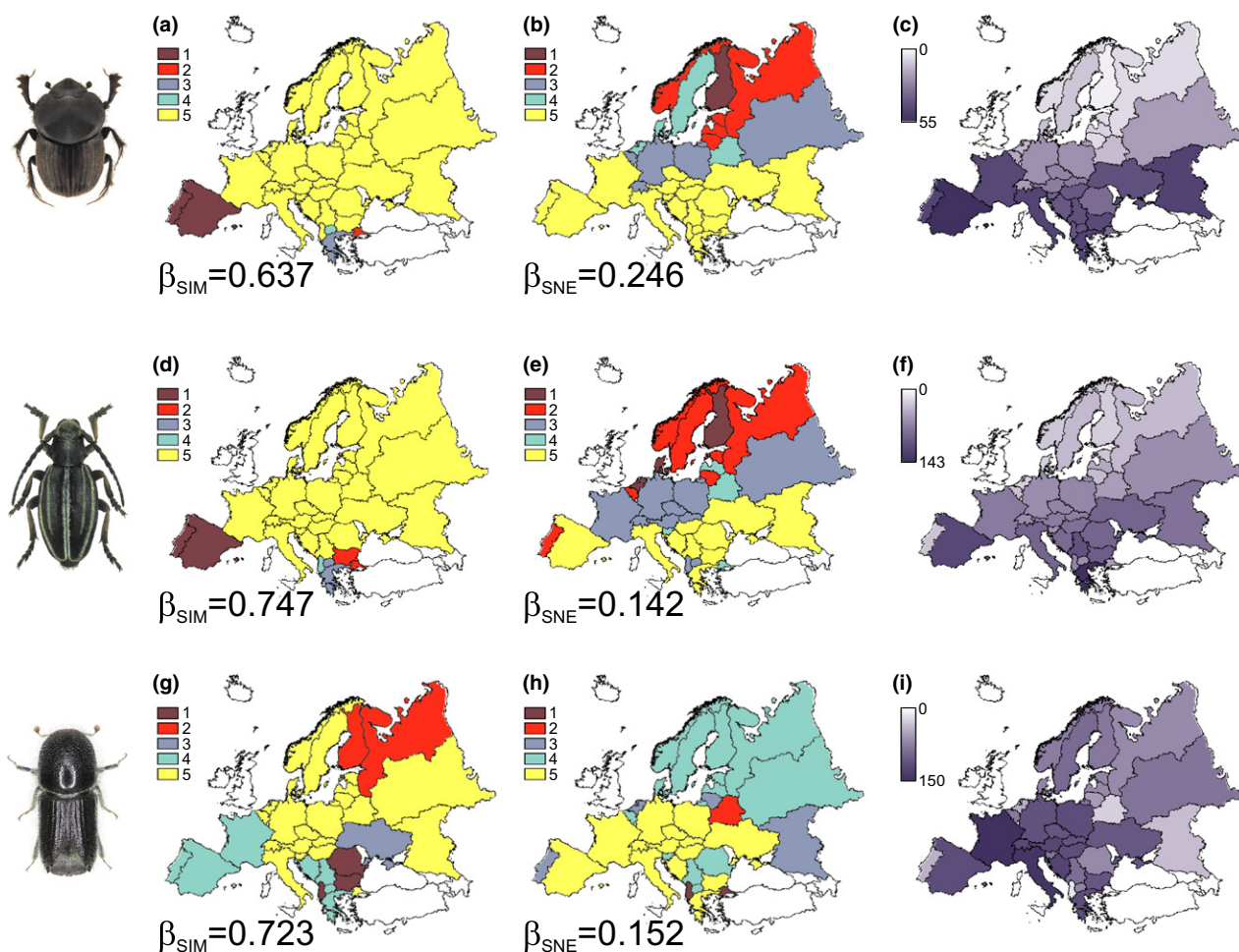


Figure 4 Differences in beta diversity patterns across beetle clades in continental Europe are exemplified with the biotic regionalizations based on pairwise dissimilarity matrices for (a, b) Scarabaeidae, (d, e) Lamiinae and (g, h) Scolytinae. Regionalization is based on (a, d, g) the pairwise turnover and (b, e, h) pairwise nestedness-resultant dissimilarity patterns, via hierarchical clustering with average linkage rule and mapping the five major clusters (see Appendix S2 for details). The species richness pattern for each clade is also shown in panels (c), (f) and (i). Beetle pictures were downloaded from Wikimedia Commons (under Creative Commons license, author Udo Schmidt).

hypotheses. While both the proportion of apterous species and the mean size had a significant contribution within the dispersal hypothesis, for the ecology hypothesis, only the trophic trait was significant in the turnover pattern (β_{sim}) and habitat type in the nestedness-resultant pattern (β_{sne}).

The reduced dataset (territories larger than 100,000 km²) yielded markedly similar results (see Appendix S3).

DISCUSSION

The analysis of beta diversity patterns of beetles showed marked differences among clades in terms of both their overall compositional heterogeneity and their multivariate pairwise structure of compositional dissimilarities. Given that these beetle clades have different dispersal abilities and ecological traits, the differences in beta diversity patterns can be used to disentangle the potential effects of dispersal and niche-based processes. For example, Scarabaeidae and Scolyt-

inae show contrasting values for overall compositional heterogeneity and pairwise dissimilarity structure (Fig. 4). For Scarabaeidae, major faunal replacement (spatial turnover) occurs in the Iberian and Balkan peninsulas, while the remaining European territories are mostly homogeneous in their beetle assemblages (Fig. 4a, Appendix S2). The pattern for nestedness-resultant dissimilarity in Scarabaeidae shows a clear latitudinal pattern of species loss from south to north (Fig. 4b, Appendix S2). The turnover pattern suggests a strong influence of Pleistocene glaciations on dung beetle distributions because spatial turnover is mostly linked to southern areas and not structured in climatic belts as would be predicted by niche theory (Hutchinson, 1957; Nekola & White, 1999). On the other hand, the latitudinal pattern of species loss would be consistent either with niche conservatism and species filtering to the north (Hawkins *et al.*, 2006; Hawkins, 2010; Hortal *et al.*, 2011) or with a pattern of incomplete post-glacial recolonization of northern regions

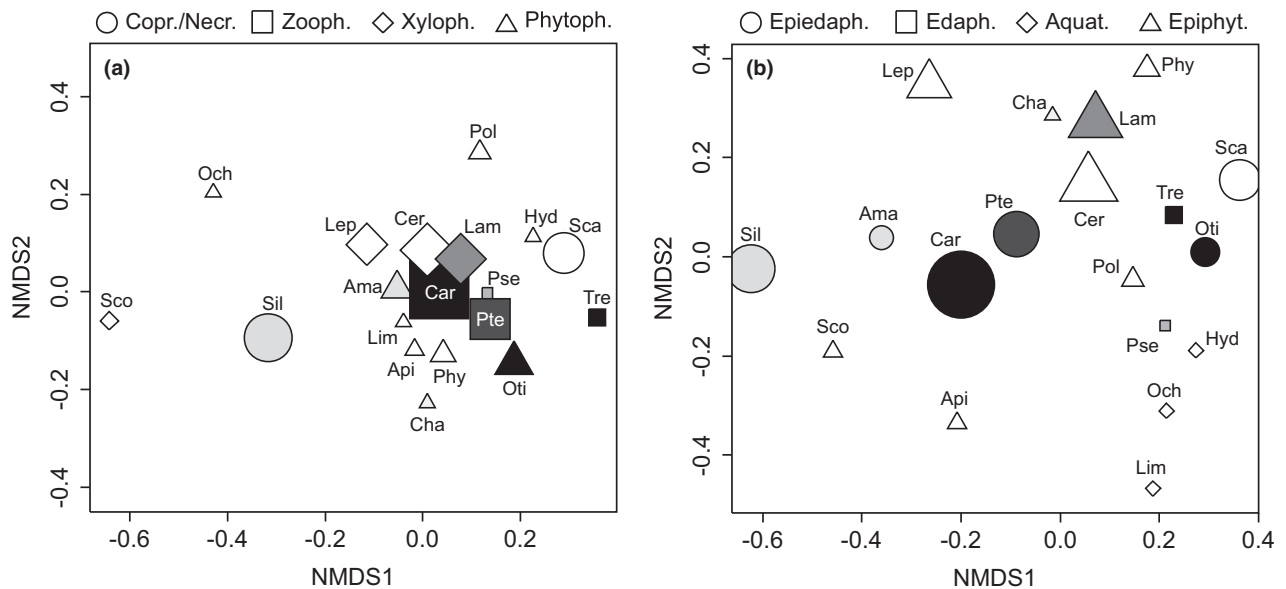


Figure 5 Non-metric multidimensional scaling (NMDS) representation of the congruence in multivariate pairwise dissimilarity patterns of beetle clades in continental Europe. The results are presented for (a) the turnover and (b) nestedness-resultant components of beta diversity. The size of the circles corresponds to body size, and the proportion of apterous species is represented in a grey scale (white is 0% and black is 100% apterous). Symbols correspond to (a) trophic trait (i.e. coprophagous/necrophagous, zoophagous, xylophagous, phytophagous) or (b) habitat type (i.e. epiedaphic, edaphic, aquatic and epiphytic).

from southern refugia controlled by limited dispersal processes (Svenning & Skov, 2007; Svenning *et al.*, 2008; Baselga *et al.*, 2012). However, the subfamily Scolytinae shows a different picture. In the scolytids, a clear latitudinal pattern of spatial turnover is evident (Fig. 4g), suggesting a strong influence of niche processes whereby species composition is determined by abiotic (e.g. climate) and biotic variables (e.g. association with different forest types). The strong influence of niche processes is likely enhanced by the well-developed dispersal abilities of the scolytids, which allow them to track favourable conditions, and, thus, their distributions are in equilibrium with their niches. This interpretation is supported by the fact that scolytid species are limited to a relatively narrow range of host tree species and undergo an obligatory dispersal during each generation (Costa *et al.*, 2013). Moreover, individuals can disperse up to 100 km in a single day via high-altitude flights (Jackson *et al.*, 2008), suggesting that most scolytid species ranges are most likely in equilibrium with their suitable environmental conditions. Therefore, dispersal limitation and post-glacial recolonization processes would not play a major role in this subfamily due to its great dispersal abilities (Baselga *et al.*, 2012). This is likely to be the causal factor behind the less marked latitudinal pattern of nestedness-resultant dissimilarity (Fig. 4h) and a flat, not significant latitudinal richness gradient (Baselga *et al.*, 2012).

Differences in beta diversity among clades were related to dispersal and ecological traits. However, results differed for overall compositional heterogeneity and multivariate pairwise structure. When overall compositional heterogeneity was considered, both dispersal and ecological traits explained a

significant proportion of variation among clades for spatial turnover and for nestedness-resultant dissimilarity. This large fraction of shared variation suggests a strong correlation between dispersal ability and ecological specialization in accordance with the hypotheses developed by Jocque *et al.* (2010). In contrast, the assessment of multivariate patterns of pairwise dissimilarity reveals a different story. The cross-taxon congruence in multivariate pairwise structures is also related to dispersal and ecological traits, but the amount of unexplained variation is larger, suggesting that stochastic, historical or other unmeasured factors may have a greater influence when the fine structure of variation in species composition among European beetle faunas is analysed. More importantly, the fractions of variation in the multivariate pairwise structure explained by dispersal and ecological traits are different (i.e. not shared), implying that both hypotheses are relevant, but their causal mechanisms may be independent. In other words, different beetle clades show different patterns of assemblage dissimilarity between pairs of European territories, and these differences are related either to the dispersal ability or to the ecological specialization of clades but not to both simultaneously. The fact that the variation in overall compositional heterogeneity is jointly explained by both hypotheses, but the variation in multivariate pairwise structures is independently explained by either one or another set of predictors may be unexpected. However, the analysis of overall compositional heterogeneity assesses whether clades differ in the total amount of faunistic heterogeneity across multiple territories, while the analysis of multivariate patterns of pairwise dissimilarity evaluates whether the specific differences among those territories are

correlated across clades (as illustrated in Fig. 1). Therefore, both variances do not need to be linked.

Two potential limitations of our study, particularly regarding the large amount of unexplained variation in multivariate dissimilarity patterns, are the potential unequal sampling effort among study units and the coarse and unequal grain size of our study units. These potential sources of error may have reduced the explanatory ability of our models. Regarding sampling effort, our data came from a comprehensive compilation of faunistic records (Löbl & Smetana, 2003, 2004; Danilevsky, 2007; Löbl & Smetana, 2010 and the Fauna Europaea database, <http://www.faunaeur.org>). All of these sources register the known presence of species in European countries, but the reliability of species absence (or, more precisely, the lack of documented presence) could not be tested. Therefore, our results contain some degree of uncertainty. However, a more complete dataset is currently unavailable so our analyses are a first attempt intended to extract novel inferences from the comparison of beta diversity patterns among multiple clades with multiple dispersal and ecological traits. This approach could be refined in future studies with better data. Regarding unequal unit size, complementary analyses performed with a more homogeneous dataset (i.e. only large territories, area > 100,000 km²) yielded similar results. Additionally, for many groups in Europe, variation in grain size is known to have minimal effects on the explanatory models for species richness (Nogués-Bravo & Araújo, 2006). Moreover, because sampling units (and size variation among them) are exactly the same in all the clades compared in this study, the disparities between patterns of variation in species composition across clades are most likely reflecting real cross-taxon variation.

In conclusion, our results indicate that the overall compositional heterogeneity in a clade is simultaneously related to the variation in clade traits assumed to reflect dispersal ability (flightlessness and body size) and ecological specialization (habitat and trophic position). In turn, the details in the dissimilarity pattern between territories are independently related to one type of trait or another and also subject to other unmeasured processes. Interestingly, within the ecology hypothesis, differences in patterns of variation in spatial turnover are related to trophic traits, while differences in patterns of variation in nestedness-resultant dissimilarity are related to habitat. Therefore, differences in trophic traits may influence faunal replacements among territories, while differences in the habitat exploited by clades may influence the degree of species loss among territories. In our opinion, a simple interpretation of these correlations allows a first insight into the dispersal and niche processes driving the variation in beta diversity patterns among clades. It is true, however, that the relationship between traits and processes could be more complex. For example, body size may also be a proxy of other ecological processes not necessarily linked to dispersal, or future studies may find a correlation between ecological niches and flightlessness. These complexities can only be addressed with sufficient distributional, morphologi-

cal, physiological and ecological data. Few previous studies have addressed the relationship between clade traits and beta diversity (e.g. Steinitz *et al.*, 2006; Sojininen *et al.*, 2007a; Qian, 2009), and, to our knowledge, none of them assessed the variation in multivariate pairwise dissimilarity structures among clades. The novel approach used in our study can provide additional information because it attempts to isolate the potential effects of different niche and dispersal processes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Presence/absence data used in this study.

Appendix S2 Ordination and classification of European territories based on 19 beetle clades.

Appendix S3 Supplementary analyses using only the largest 18 territories (> 100,000 km²).

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